Chapter 2

CULTURE IN NON-HUMAN PRIMATES

DEFINITIONS AND EVIDENCE

Tatyana Humle and Nicholas E. Newton-Fisher

Definitions

The attribution of culture to non-human animals has been controversial and continues to fuel much heated debate (Galef 1992; Kendal 2008). Much of this debate hinges on how culture is defined. In 1952, Kroeber and Kluckhohn compiled a comprehensive review of how the term culture had been used in modern times up until the early 1950s. They collated 168 definitions, all implying a human prerogative, and exemplified by Tyler's classic definition of culture as 'that complex whole which includes knowledge, belief, art, morals, custom, and any other capabilities and habits acquired by man as a member of society' (Tyler 1871: 1). Kant (1786) was highly influential in originally formulating this human-centric concept of culture as that 'artifice unique to man which has permitted human beings to escape their natural animality and express their rational [and moral] humanity [... and] their freedom from the laws of nature' (Arnhart 1994: 476). The anthropological concept of culture centres on the idea that culture is learned, rather than biologically inherited, cross-generational, adaptive, and based on systems of arbitrarily assigned meanings that are shared by a society. Anthropological definitions therefore typically refer specifically to the human nature of culture centred on language, symbols,

teaching and imitation (Tomasello 1999). Human-centric definitions of culture therefore leave little or no room for understanding the evolutionary origins of human culture. In their strictest sense they also reject the possibility for culture among early hominins: the australopithicines and *Homo habilis* (McGrew 1992; Lycett 2011; see also Lycett, this volume).

The supremacy of *Homo sapiens* in all domains pertaining to material and social intelligence and culture was only challenged a century after Darwin's publication of the *Descent of Man* in 1871. The diversity and complexity of bird songs fascinated and amazed Darwin; based on his extensive travels and observations, he had noted 'that an instinctive tendency to acquire an art is not peculiar to man' (p. 56). Darwin also cited Savage and Wyman (1843–44), stating 'it has often been said that no animal uses any tool; but the chimpanzee in a state of nature cracks a native fruit, somewhat like a walnut, with a stone' (Darwin 1871: 51). Nevertheless, six decades passed before another eminent scientist, the influential American cultural anthropologist Alfred L. Kroeber, would contemplate the possibility of culture in non-human animals, and apes in particular (Kroeber 1928; Kroeber and Kluckhohn 1952). The birth of Japanese primatology in the late 1940s led to the coining of terms such as 'sub-culture' and 'preculture', applied to the descriptions of potato washing among Japanese macaques (*Macaca fuscata*) of Koshima Island (Kawamura 1959: 43). A decade later, Kummer (1971: 11), a Swiss ethologist and behavioural scientist, employed – possibly for the first time – the term 'culture' in relation to non-human animals.

Besides the pioneering studies of Imanishi, Itani and Kawamura (Matsuzawa and McGrew 2008), Goodall's (1973), and McGrew and Tutin's (1978) first reports of behavioural variations among wild chimpanzees (*Pan troglodytes*) in East Africa were milestones in the study of culture in non-human animals. These studies inspired numerous publications on behavioural diversity among wild non-human primates, especially chimpanzees. Cumulatively, these observations led in the late 1990s to the emergence of 'cultural primatology' as a distinct discipline (de Waal 1999).

~~The~~ studies also paved the way for more encompassing definitions of culture and for a comparative approach to the study of the roots of human culture. The broader definitions employed by many primatologists, biologists, psychologists and anthropologists range from deceptively simple ones such as culture as 'the way we do things' (McGrew 2003: 433) to more operational ones viewing culture as 'all group-typical behaviour patterns, shared by members of animal

communities, that are to some degree reliant on socially learned and transmitted information' (Laland and Hoppitt 2003: 151).

Most researchers would agree that culture consists of behaviours that are (a) transmitted within groups, communities or populations via some form of social learning mechanism, (b) temporally maintained across successive generations and (c) vary in their expression or form between social groupings. The perception of culture as 'a system of socially transmitted behaviours' (van Schaik et al. 2003a: 102) stimulated a great deal of interest in the study of behavioural variation and imitative abilities among our closest living relatives – the non-human primates (hereafter, primates), especially the chimpanzee. In parallel, a number of studies revealed the prevalence of socially transmitted behavioural variants across a wide range of taxa including insects, fish, birds and cetaceans (reviewed by Fragaszy and Perry 2003; Lonsdorf and Bonnie 2010; see also Laland, this volume).

A host of experimental studies have shown cultural capacities – social learning and in some cases diffusion of a novel behaviour – in a variety of primate species, from new world monkeys (e.g. cotton-top tamarins *Saguinus oedipus*: Humle and Snowdon 2008; marmosets *Callitrix jacchus*: Voelkl and Huber 2000; capuchins ~~*Cebus*~~ *apella*: Dindo et al. 2008) to apes, particularly chimpanzees (reviewed by Whiten et al. 2004; Hopper et al. 2007; Horner 2010; Lonsdorf and Bonnie 2010). Capuchins, and chimpanzees in particular, are capable of transmitting behaviour(s) with a relatively high degree of fidelity along a sequential chain of individuals or even – at least in chimpanzees – between groups (Horner et al. 2006; Hopper et al. 2007). Whether the propensity of chimpanzees and capuchins for culture surpasses that of other primates will likely be clarified as more data emerge from macaques and other species, such as orang-utans (*Pongo* spp.) who exhibit cultural capacities in the wild (van Schaik et al. 2003a, 2003b; Fox et al. 2004; Jaeggi et al. 2007). Such studies have clarified the mechanisms of social learning, and revealed important constraints posed by: the saliency and social relationship of the demonstrator(s) to the naïve individual(s); the possibility for co-action or joint interaction; the type of actions or degree of complexity presented by the task; the presence or absence of food in the experimental design; the duration and frequency of exposure; and the age and sex of the subjects used.

Studies in captivity have markedly contributed to our understanding of the capacity for social learning and transmission of behaviour, but they have ~~unfortunately~~ revealed little about the influences of the physical and social setting on behavioural diffusion and dissemination, and of behavioural interactions between

knowledgeable and naïve individuals on the learning trajectory of young. They have also placed much of the emphasis in the identification of culture on the existence of social transmission of a specific, often contrived, behaviour. While this has broadened the species and behaviours that have been considered 'cultural', it arguably weakens the usefulness of comparative studies in understanding the evolutionary origins of human culture.

The attribution of differences in behavioural patterns to culture in wild primates has been critiqued for failing to consider more parsimonious explanations (Galef 1992; Tomasello 1999; Ingold 2001; Laland and Janik 2006; Laland, Cowie and Morgan, this volume). The critics maintain that none of the reported putative cultural variants among wild primates can irrefutably be attributed to social learning rather than genetic or environmental factors. It is the case that translocation experiments of a kind necessary to refute categorically environmental and genetic influences in explaining observed variations in behaviour (e.g. Helfman and Schultz 1984; see Laland, Cowie and Morgan, this volume) are typically not feasible for field primatologists, in part for ethical reasons. The extended life histories of primates, especially among great apes, also pose considerable logistical difficulties that constrain our ability to infer culture and to investigate patterns of transmission and maintenance of behavioural patterns across generations. Nevertheless, field studies have provided evidence of social transmission, and as we argue below, are critical to a comparative understanding of culture.

In this context it is important to recognize and distinguish between a 'tradition', which we define for our immediate purposes as a socially transmitted behaviour that varies in its form between groups, and a 'culture'. If the term 'culture' is to avoid becoming redundant through synonymy with the presence of social learning, and if it is to be a concept usefully applied to both human and non-human animals, it must refer to more than a single tradition. The use in humans, across particular definitions, provides a collective description of the behavioural variation between groups: behaviours that are shared among group members, persistent across generations, not merely being transmitted socially. Moreover, culture in humans typically refers to a collection of socially transmitted behavioural variants – an array of shared, persistent traditions – that span a number of domains. Social learning may be a key mechanism by which behavioural variants are spread, and how traditions are created and maintained, but it is the presence of this cross-domain array of shared, persistent traditions that defines culture. To return to McGrew's (2003) definition, culture is 'the way we do *things*'.

Cultural Primatology: Insights from the Field

Identifying Cultures

Investigation of culture in primates has focused on the process of social transmission using experiments with captive animals, and on the identification of putative cultural variants within and between wild-living populations. This identification process, based on the detection of geographic variations in behaviour, is referred to variously as the ethnographic method (Wrangham et al. 1994), group comparison (Fragaszy and Perry 2003) or the method of elimination (van Schaik et al. 2003a). A behaviour is classed as a possible cultural variant if it occurs sufficiently frequently in one or more populations or social groups to be consistent with social transmission, and yet is absent in one or more other groups of the same species where environmental explanations for such absence can be rejected (cf. Whiten et al. 1999, 2001).

The production of comprehensive group- or community-specific ethograms often requires decades of field presence. The collection of exhaustive lists of behavioural variants depends, on the one hand, on research effort across seasons and years, and the number of observers *in situ*, and on the other hand, on the frequency of occurrence of behaviours, observation conditions or, for tool use, the reliability with which we can infer behaviour based on artefacts. For instance, it took more than three decades of research to produce a comprehensive list of tool-use behaviours among the chimpanzees of Bossou (Figure 2.1).

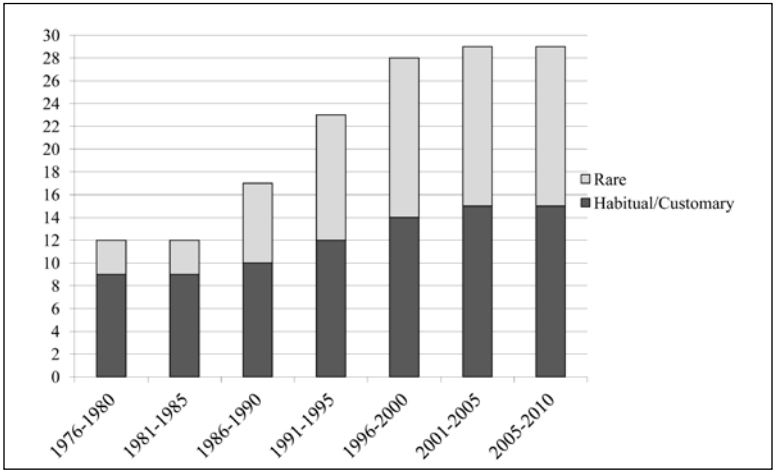

Figure 2.1. Cumulative number of observed rare, habitual and customary tool-use behaviours recorded among the chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. For definitions of 'rare', 'habitual' and 'customary' see Whiten et al. 1999.

As many as six customary tool-use behaviours were initially unnoticed as a consequence of seasonal biases in research effort and poor levels of habituation during the first decade and a half of research (Matsuzawa et al. 2011).

Nevertheless, systematic and detailed fieldwork has enabled us to appreciate better the impressive within-species variability in behaviour across a range of domains. The classic examples of sweet-potato washing and wheat sluicing among the Japanese macaques of Koshima (summarized in Hirata et al. 2001) or the stone-handling patterns of Japanese macaques (Leca et al. 2007) suggest further that primates can build on earlier achievements and socially transmit those novel behaviours to other group members. Do these examples demonstrate the 'ratchet effect' at work, an effect proposed as a distinguishing characteristic of human culture (Tomasello 1999)? The 'ratchet effect' in material culture implies cumulative modifications and incremental improvements thus resulting in increasingly elaborate technologies. Indirect, but perhaps compelling, evidence for cumulative cultural evolution in wild chimpanzees comes from the enormous variability in tool-use techniques, such as for termite fishing and ant dipping.

Ant dipping is one of the most widespread uses of sticks as tools among wild chimpanzees. The targeted army ants (*Dorylus* sp.) are ubiquitous across Africa, and while several wild chimpanzee communities exhibit this behaviour, some such as the Sonso community in Budongo do not. Across the communities who do target these ants there is further variation, for example in the length of the wands used, and in the context in which the behaviour is displayed (dipping for ants at their nest versus when in a column or hunting). Perhaps unsurprisingly, chimpanzees use longer tools when targeting ants at their nests (when they are more aggressive) or targeting inherently more aggressive species (Humle and Matsuzawa 2001; Schoning et al. 2008). Tool length, in turn, is a likely influence on the technique used to remove ants from the tool: *direct mouthing* of shorter tools through the mouth/lips, or *pulling-through* of longer tools through the closed fingers of one hand and then bringing the ants to the mouth (Humle and Matsuzawa 2002). Moebius et al. (2008) showed that, despite the influence of prey ecology on the variation in tools employed, neither prey behaviour, characteristics, availability or density could account for all variation in ant dipping behaviour between the chimpanzees of Bossou and those of the Taï forest, Côte d'Ivoire. They conclude that these differences must therefore be cultural. This set of studies highlights the intricate ~~narrow~~ inter-relationship between ecology and culture (Humle 2010).

Furthermore, while chimpanzees typically use a single tool, a dipping probe, to harvest army ants, chimpanzees in the Goualougo Triangle, Republic of Congo, use a 'tool-set' – the serial use of more than one type of tool to achieve a goal (Brewer and McGrew 1990) – in army ant predation (Sanz et al. 2010). This tool-set combines a puncturing tool and 'dipping' probe, and differs from other types of tool combinations used by these chimpanzees to prey upon termites or gather honey (Sanz and Morgan 2007, 2009; Sanz et al. 2010). The use of a tool-set is thought to improve harvesting efficiency and prey exploitation over longer periods of time. In the case of army ant predation, the use of a tool-set minimizes the risk of eliciting the colony's premature migration and desertion from the nest (Sanz et al. 2010).

Systematic collation of behavioural differences across long- to medium-term field studies has generated profiles for social groups that represent arrays of putative cultural behaviour in a number of primate species. Socially learned traditions have been proposed in relation to food processing techniques, tool uses and social conventions in wild capuchin monkeys (*Cebus* spp.: Panger et al. 2002; Perry et al. 2003; Ottoni and Izar 2008; Mannu and Ottoni 2009) and in stone-handling patterns in Japanese macaques (*Macaca fuscata*) (Leca et al. 2007). Researchers have so far recognized at least thirty-nine candidates for cultural variants in chimpanzees (Whiten et al. 1999), fourteen in bonobos (*Pan paniscus*) (Hohmann and Fruth 2003) and twenty-four in orang-utans (van Schaik et al. 2003a). Recorded numbers of putative cultural variants are likely to increase as more groups, communities and populations are studied, and as researchers pay more careful attention to subtle behavioural details.

The putative cultural variants in great apes range across a wide spectrum of behavioural domains, including foraging, tool use, communication, defence, self-maintenance, and social customs. These great ape species therefore demonstrate arrays of behavioural variants, each variant a good candidate for transmission by social learning. Even if rigorous demonstration of social learning for each of those variants is lacking, positing the existence of culture as an explanation for these behavioural variants remains a sensible working hypothesis. Without it, why should we look for evidence of social transmission, and how would we know which behaviours were good candidates for such an investigation? Without it, we would fail to appreciate the depth of behavioural diversity prevalent among social groups – to our ignorance and, given the precarious conservation status of these species, to their detriment.

Identifying Social Transmission in the Field

Primates are long-lived with extended inter-birth intervals, ranging in the great apes from a mean of 5.6 years in chimpanzees to 7.7 years in orang-utans (*Pongo* sp.) in their natural habitat (Wich et al. 2009). They also have long periods of maturation and development during which young acquire and perfect skills and behaviours, which are often, but not always, essential to their survival and key to managing life in a group. For example, Bossou chimpanzees typically do not demonstrate first success in combining anvil and hammer stones to crack oil-palm nuts (*Elaeis guineensis*) before the age of 3.5 to 5 years (Inoue-Nakamura and Matsuzawa 1997), and take another 3 to 5 years to attain an adult level of proficiency (Biro et al. 2006).

It may take years, therefore, to amass the necessary longitudinal and cross-sectional data necessary to gain some understanding of the developmental trajectory of young individuals, and the degree to which behaviours are socially transmitted. It took 163 days, spread across four years, for Lonsdorf (2006) to gather the necessary data to evaluate maternal contribution to the acquisition of termite fishing behaviour among chimpanzees (*P. t. schweinfurthii*) of the Gombe National Park in Tanzania. Similarly, Humle et al. (2009) required data across eight years to explore social learning influences on the acquisition of ant dipping among the chimpanzees of Bossou.

The Humle et al. (2009) study provided good evidence for social learning. She found that mothers were the prime models for their offspring during the first five years of their life. Since infants whose mothers are keen ant dippers have the opportunity to observe ant dipping earlier, they acquired the ant dipping behaviour sooner than those whose mothers dipped less frequently, and were also more efficient in this behaviour that others of the same age. Across infants, as performance improved, time spent observing ant dipping being performed decreased.

Perry (2009) conducted a seven-year-long study to investigate social influence on the acquisition of food processing techniques of *Luehea candida* fruits among wild white-faced capuchins (*Cebus capucinus*). The two techniques recorded to extract the seeds were equally efficient. Female infants, as with the chimpanzees in Lonsdorf's (2006) study, were more likely than male infants to match their mother's technique. Overall, individual capuchins typically settled on the technique they most frequently observed.

Jaeggi et al. (2010) accumulated nearly two thousand observation hours to explore social learning of diet and foraging skills among immature wild Bornean orang-utans (*Pongo pygmaeus wurmbii*). The diets of immature orang-utans were essentially identical to their mothers', even though mothers differed in their diets. Direct teaching

was never recorded, but immature orang-utans selective observation of their mothers performing extractive foraging tasks guided their practice and acquisition of these complex skills. These data nicely complement records of 'traditional' dietary differences among Bornean orang-utan populations (Bastian et al. 2010).

However painstaking the research process, and despite the absence of control conditions, such studies provide convincing evidence for the role of social learning in the diffusion (within the social unit) and maintenance of group-typical behaviours among wild primates. The real bonus of this approach lies in its social and ecological contextual validity. It presents enormous potential in helping us to elucidate influential factors which may either hinder or promote diffusion of cultural variants, including the role of ecological and social opportunity, and also to address potential patterns of sex differences in learning trajectories.

Field-based Experiments

In this approach, exemplified by the work of Matsuzawa and colleagues, researchers stimulate the occurrence of tool-use behaviours in a locale within the natural range of the wild population or group under study. This setting is equivalent to an outdoor 'laboratory' where tools, food availability, distribution and type can readily be manipulated, and observational conditions are maximized (e.g. chimpanzees: Matsuzawa 1994; bearded capuchins *~~Cebus~~ libidinosus*: Fragaszy et al. 2010). At Bossou, reliable, consistent longitudinal data on chimpanzee tool use has been gathered over the course of several weeks per year since 1988 for oil-palm nut cracking, and since 2000 for water drinking with leaves (Inoue-Nakamura & Matsuzawa 1997; Tonooka 2001; Biro et al. 2003, 2006; Sousa et al. 2009).

These experiments have yielded insights into the acquisition of nut cracking (Inoue-Nakamura and Matsuzawa 1997) and water drinking (Sousa et al. 2009). Young chimpanzees acquire the skill of using leaves for drinking water at around the age of 1.5 years. Infants initially rely on leftover tools for drinking, and only begin to manufacture their own leaf tools at 3.5 years of age (Sousa et al. 2009). Stone-tool use appears more complex, and is acquired during a critical period spanning the ages of 3.5 to 5 years. During this period, young chimpanzees repeatedly observe the behaviour of able nut crackers from close range and practice the behaviour on their own (Figure 2.2), a process termed 'education by master-apprenticeship' (Matsuzawa et al. 2001). Evidence of active demonstration and assistance in canalizing an immature's acquisition of these skills was not found in the Bossou chimpanzees, but Boesch (1991) reported numerous examples from the Taï forest of chimpanzee mothers facilitating

Figure 2.2. 'Education by master-apprenticeship' during the acquisition of nut cracking at Bossou: a) a juvenile female chimpanzee, *Joya*, sits beside her mother, *Jire*, who is cracking oil palm nuts with a mobile hammer and anvil stone; b) *Joya* approaches and closely observes her mother's behaviour; c) *Joya* grabs a hammer-anvil stone set and practices nut cracking. Although she is able to successfully combine to anvil and hammer stones and the nut, *Joya* has a hard time efficiently manipulating the hammer stone to strike the nut (Photos by Boniface Zogbila, KUPRI/IREB). She will continually to repeatedly observe her mother or other proficient nut-crackers within the community until she perfect the skills on her own.

the acquisition of nut-cracking skills by their offspring, including two examples of active teaching.

Propagation of socially learnt behaviours *between groups* of primates remains poorly understood and logistically daunting to demonstrate. Field experiments have been used as an indirect approach to investigating social transmission of putative cultural variants between neighbouring chimpanzee communities. These studies indicate that dissemination of socially learned behaviours across wild chimpanzee communities does not follow a simplistic pattern of chain transmission yielding cultural zones (Biro et al. 2003; Koops et al. 2008; Gruber et al. 2009).

Cracking of oil-palm nuts with hammer stones is customary among the Bossou chimpanzees. However, it is almost certainly absent from the chimpanzee community of the Seringbara area, 6 km from Bossou, despite the presence of oil palms (Humle and Matsuzawa 2001, 2004). Koops et al. (2008) provided Seringbara chimpanzees with oil-palm nuts and suitable anvil and hammer stones across several locations that they were known to frequent. Motion-triggered cameras showed that none of the chimpanzees who encountered the nuts and stones attempted to perform nut cracking. This suggests that the lack of nut cracking in the Seringbara chimpanzee community is fundamentally due to a lack of cultural knowledge, rather than a lack of ecological opportunity (cf. McGrew et al. 1997; Humle and Matsuzawa 2004).

Nuts of *Panda oleosa* are hard to crack, but chimpanzees in the Taï forest crack them with the aid of heavy wooden or stone hammers (Boesch and Boesch 1983). This nut species does not naturally occur in the range of the Bossou chimpanzees. When Biro et al. (2003) presented Bossou chimpanzees with *Panda* nuts in the outdoor laboratory, no member of the community transferred their nut-cracking skills from oil-palm nuts to the unfamiliar *Panda* nuts. Consequently, Bossou chimpanzees failed to innovate *Panda* nut cracking (Biro et al. 2003).

The Bossou chimpanzees were also provided with *Coula edulis* nuts, a second species absent from their home range. These nuts are cracked and consumed at Taï (Boesch and Boesch 1983), as well as on the Ivorian side of the Nimba Mountains only 14 km from Bossou (Humle and Matsuzawa 2001). A clear conservatism was obvious in the chimpanzees' response. With the exception of juveniles (4–7 year olds), most members of the community initially sniffed the nuts but otherwise ignored them and continued to crack the familiar oil-palm nuts.

One exception was an adult female, Yo, who spontaneously started cracking the *Coula* nuts. Yo was recorded as an adult member of the

Bossou community when observations began in 1976. Her spontaneous cracking of *Coula* nuts was therefore either an innovation in response to the ecological opportunity created by the experiment, or evidence that she had once been a member of a community in which *Coula* nuts were cracked and consumed, memory of a behaviour not used in twenty-four years. In support of the idea that Yo transferred in from another *Coula*-nut-cracking community, she was never observed to pestle pound, despite feeding on the petiole of palm fronds: pestle pounding is complex and unique tool-using behaviour common among adult members of the Bossou community (Yamakoshi and Sugiyama 1995).

Whether an innovation or distant memory, the juveniles paid close attention to Yo's behaviour and soon began cracking the novel *Coula* nuts on their own. This behaviour eventually spread among both juvenile and adult members of the community, providing good evidence of social transmission of a novel behaviour. The conservatism of the adults and the observation that juveniles use one another, or older individuals, as models, have implications for the selection of captive subjects for experimental investigations of social transmission.

The natural conservatism of adult chimpanzees is further demonstrated in the results of recent field experiments conducted in East Africa. Gruber et al. (2009) presented two habituated communities of wild chimpanzees in Uganda – Kanyawara in Kibale and Sonso in Budongo – with drilled horizontal logs loaded with honey to stimulate honey-feeding behaviour, and used motion-triggered cameras to record the chimpanzees' response. The Sonso chimpanzees, who do not typically use stick tools but will use leaf sponging to gather water, solved this task by using leaves and/or their fingers to obtain the honey, whereas the Kanyawara community, who customarily use sticks to gather honey, employed sticks to obtain the honey contained within the log.

The Necessity of Field Studies

In a field setting, with the absence of control conditions, gathering the empirical data necessary to demonstrate social learning of cultural variants is not easy, in contrast to experiments conducted in captivity. Despite this, field studies provide the only meaningful way of establishing the array of behavioural traditions that constitute the cultures of groups living under natural social and ecological conditions, and are the best means of probing the environmental, social and development influences on behavioural transmission and variation. Studies of captive animals might establish the cultural capabilities of a species, but only field studies of wild individuals can document their cultures.

Chances for witnessing individual migration events between groups or communities and potential dissemination of putative cultural variants based on an a priori comprehensive knowledge of both the individual's and the host group or community's behavioural repertoire are few. One of the rare published examples was the introduction of a novel social grooming variant, a form of hand-clasp grooming, into the M-group of chimpanzees at Mahale, Tanzania, with the immigration of a female chimpanzee from the K-group (Nakamura and Uehara 2004). This female also adopted types of hand-clasp allogrooming displayed by members of her new community (Figure 2.3). Her immigration increased heterogeneity in this social custom in the M-group. Although cultural transmission is predicted to yield homogeneity in behaviour, this example and others across different behavioural domains suggest that chimpanzees tend to maintain idiosyncratic behavioural preferences once acquired and suited to their purposes (e.g. ant-dipping techniques among Bossou chimpanzees: Humle et al. 2009). The habituation and study of neighbouring groups and communities is gradually creating more opportunities for recording migration events that are key to understanding social diffusion and dissemination of novel behavioural variants in primates.

Field researchers are only now beginning to appreciate the possibility for cumulative cultural evolution in primates other than humans, with successive generations building on earlier achievements. Research on stone-tool use in both chimpanzees and capuchins is also starting to provide key insights into the interpretation of early hominin lithic technology (Haslam et al. 2009).

Field studies focused on understanding patterns of transmission of socially learned behaviours in wild primates are also yielding key data useful to experimental researchers working with primates in captive settings. Our current understanding of what is going on in the wild should help to develop or refine experimental paradigms and focus research onto a wider range of behavioural domains, including communication and social customs (e.g. Watson and Caldwell 2009).

Novel Approaches

Primate Archaeology

Archaeological methods have recently been applied to the study of primate material culture, focusing on the lithic technology used to crack nuts (Haslam et al. 2009). Mercader et al. (2002) provided descriptions of recent buried remains of unintentionally fractured stone and organic residues resulting from the nut-cracking activities of modern chimpanzees in the Taï forest. This study highlighted the

Figure 2.3. Examples of allogrooming in chimpanzees. a) Typical form of wrist-to-wrist hand-clasp grooming, a social custom observed among Mahale chimpanzees in Tanzania (photograph by Michio Nakamura); b) Budongo chimpanzees of the Sonso community never perform hand-clasp grooming but will groom simultaneously without this structure (photograph by Nicholas Newton-Fisher).

potential in applying archaeological methods to the study of material culture among non-human extant primates and in identifying the type of material assemblages that could characterize ancient nut-cracking sites of chimpanzees (e.g. Carvalho et al. 2008, 2009). Chimpanzees and humans share several important elementary technological attributes, including the transport of stones to cracking sites, the optimal combination of locally available raw materials, size, shape and weight criteria to efficiently crack a given species of nut, and the accumulation and concentration of stones, flake and shell remains resulting from percussive activities at specific sites within the landscape. Excavated sites can be dated by standard archaeometric techniques, such as radiocarbon dating. Chimpanzee sites excavated thus far have ranged from hundreds (Mercader et al. 2002) to thousands (Mercader et al. 2007) of years old.

No sites of wild capuchins have yet been excavated in this manner. However, emerging data indicate that capuchin monkeys use hard level surfaces, including large embedded stones or wooden logs, as anvils, and mobile stones as hammers to crack open palm nuts, and transport hammer stones as well as nuts to anvil sites (Visalberghi et al. 2007). Wild capuchins thus provide an additional point of reference for interpreting hominin stone assemblages. Stone handling during play, and stone throwing in Japanese macaques, also represent group-specific behavioural traditions, which are shedding some important insights into the evolution of stone technology in hominids (Leca et al. 2007).

Cladistic Analysis

Cladistic analysis techniques traditionally applied to evolutionary biology have proved useful in explaining diversity in human material culture (Collard 2010; Lycett 2010). Lycett et al. (2007, 2010) have recently applied this phylogenetic analytical method to the accumulated database of cultural arrays across chimpanzee communities to help to refute the hypothesis that genetic differences underlie reported behavioural differences among chimpanzee communities. Some researchers are now using these results and methods to ask specific questions, such as what is the correlation between group size and the number of putative cultural traits across chimpanzee communities. Lind and Lindenfors (2010) have ~~thus~~ suggested that it correlates with the number of females within communities, but not with the number of males. Their result agrees with observational studies and our knowledge of wild chimpanzees: maternal (vertical) transmission and female emigration are indispensable in promoting behavioural diffusion and dissemination in chimpanzees.

The gradual accumulation of datasets or studies of the ontogeny of behavioural acquisition, group demographics and social dynamics, feeding ecology and so on, are providing increased opportunities for meta-analytical studies and refinements to models of cultural transmission. The next step is to feed in the empirical data and generate new testable hypotheses.

The Future of Cultural Primatology

Cultural primatology is still in its infancy. Future field studies – both observational and experimental – together with experiments using captive subjects, are likely to yield many more insights into the cultural propensities of primates, how these and non-primate cultures differ from those of humans, and how social dynamics, ecology and demographics shape culture and the diffusion and dissemination of socially learned behaviours. This will increasingly be the case as additional data are collected and more refined analyses and meta-analyses conducted. A major challenge is also our surprisingly limited understanding of cultural transmission processes in humans, but anthropologists and psychologists are rapidly filling this knowledge gap (e.g. Caldwell and Millen 2009, 2010). New statistical methods are also being developed and tested which should help us to identify more readily the spread of behavioural innovations through social transmission (Hoppitt et al. 2010). It is also essential that experimental (comparative) psychologists ask questions and frame experiments using growing insights from field-based studies. Similarly, primatologists in general need to be more attentive to models and hypotheses generated beyond the field of primatology, and should seek to gather the necessary empirical data with which to test the predictions of such models (e.g. Laland and Kendal 2003).

References

Arnhart, L. 1994. 'The Darwinian Biology of Aristotle's Political Animals', *American Journal of Political Science* 38(2): 464–85.

Bastian, M.L, N. Zweifel, E.R. Vogel, S.A. Wich and C.P. van Schaik. 2010. 'Diet Traditions in Wild Orangutans', *American Journal of Physical Anthropology* 143(2): 175–87.

Biro, D., N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi, C. Sousa and T. Matsuzawa. 2003. 'Cultural Innovation and Transmission of Tool-use in Wild Chimpanzees: Evidence from Field Experiements, *Animal Cognition* 6: 213–23.

_____.C. Sousa and T. Matsuzawa. 2006. 'Ontogeny and Cultural Propagation of Tool Use by Wild Chimpanzees at Bossou, Guinea: Case Studies in Nut Cracking and Leaf Folding', in T. Matsuzawa, M. Tomonaga and M. Tanaka (eds), *Cognitive Development in Chimpanzees*. New York: Springer, pp. 476–508.

Boesch, C. 1991. 'Teaching among Wild Chimpanzees', *Animal Behaviour* 41: 530–32.

_____ and H. Boesch. 1983. 'Optimisation of Nut Cracking with Natural Hammers by Wild Chimpanzees', *Behaviour* 83(3–4): 265–86.

Brewer, S.M. and W.C. McGrew. 1990. 'Chimpanzee Use of a Tool-set to Get Honey', *Folia Primatologica* 54: 100–4.

Caldwell, C.A., and A.E. Millen. 2009. 'Social Learning Mechanisms and Cumulative Cultural Evolution: Is Imitation Necessary?', *Psychological Science* 20(12): 1478–83.

_____ and A.E. Millen. 2010. 'Human Cumulative Culture in the Laboratory: Effects of (Micro) Population Size', *Learning and Behavior* 38(3): 310–18.

Carvalho, S., D. Biro, W.C. McGrew and T. Matsuzawa. 2009. 'Tool-composite Reuse in Wild Chimpanzees (*Pan troglodytes*): Archaeologically Invisible Steps in the Technological Evolution of Early Hominins?, *Animal Cognition* 12: S103–14.

_____.E. Cunha, C. Sousa and T. Matsuzawa. 2008. 'Chaines Operatoires and Resource-exploitation Strategies in Chimpanzee (*Pan troglodytes*) Nut Cracking', *Journal of Human Evolution* 55(1): 148–63.

Collard, M. 2010. 'Integrating Anthropological Genetics with Cultural Anthropology and Archaeology: New Opportunities', *Journal of Anthropological Science* 88: 239–42.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Dindo, M., B. Thierry and A. Whiten. 2008. 'Social Diffusion of Novel Foraging Methods in Brown Capuchin Monkeys (*Cebus apella*)', *Proceedings of the Royal Society B-Biological Sciences* 275(1631): 187–93.

Fox, E.A., C.P. van Schaik, A. Sitompul and D.N. Wright. 2004. 'Intra- and Interpopulational Differences in Orangutan (*Pongo pygmaeus*) Activity and Diet: Implications for the Invention of Tool Use', *American Journal of Physical Anthropology* 125(2): 162–74.

Fragaszy, D.M., R. Greenberg, E. Visalberghi, E.B. Ottoni, P. Izar and Q. Liu. 2010. 'How Wild Bearded Capuchin Monkeys Select Stones and Nuts to Minimize the Number of Strikes per Nut Cracked', *Animal Behaviour* 80(2): 205–14.

_____ and S.E. Perry. 2003. *The Biology of Traditions: Models and Evidence*. Cambridge University Press.

Galef, B.G. 1992. 'The Question of Animal Culture', *Human Nature* 3: 157–78.

Goodall, J. 1973. 'Cultural Elements in a Chimpanzee Community', in E.W. Menzel (ed.), *Precultural Primate Behaviour*. Basel: Karger. pp. 195–249.

Gruber, T., M.N. Muller, P. Strimling, R. Wrangham and K. Zuberbuhler. 2009. 'Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task', *Current Biology* 19(21): 1806–10.

Haslam, M., A. Hernandez-Aguilar, V. Ling, S. Carvalho, I. de la Torre, A. DeStefano, A. Du, B. Hardy, J. Harris, L. Marchant et al. 2009. 'Primate Archaeology', *Nature* 460: 339–44.

Helfman, G.S. and E.T. Schultz. 1984. 'Social Tradition of Behavioural Traditions in a Coral Reef Fish', *Animal Behaviour* 32: 379–84.

Hirata, S., K. Watanabe, M. Kawai and T. Matsuzawa. 2001. '"Sweet-potato Washing" revisited', in T. Matsuzawa (ed.), *Primate Origins of Human Cognition and Behavior*. Tokyo: Springer-Verlag, pp. 487–508.

Hohmann, G. and B. Fruth. 2003. 'Culture in Bonobos? Between-species and Within-species Variation in Behavior', *Current Anthropology* 44: 563–71.

Hopper, L.M., A. Spiteri, S.P. Lambeth, S.J. Schapiro, V. Horner and A. Whiten. 2007. 'Experimental Studies of Traditions and Underlying Transmission Processes in Chimpanzees', *Animal Behaviour* 73: 1021–32.

Hoppitt, W., N.J. Boogert, and K.N. Laland. 2010. 'Detecting Social Transmission in Networks', *Journal of Theoretical Biology* 263(4): 544–55.

Horner, V. 2010. 'The Cultural Mind of Chimpanzees: How Social Tolerance can Shape the Transmission of Culture', in E.V. Lonsdorf, S.R. Ross and T. Matsuzawa (eds), *The Mind of the Chimpanzee*. Chicago and London: University of Chicago Press, pp. 101–15.

_____.A. Whiten, E. Flynn and F.B.M. de Waal. 2006. 'Faithful Replication of Foraging Techniques along Cultural Transmission Chains by Chimpanzees and Children', *Proceedings of the National Academy of Sciences of the United States of America* 103(37): 13878–83.

Humle, T. 2010. 'How are Army Ants Shedding New Light on Culture in Chimpanzees', in E.V. Lonsdorf, S.R. Ross and T. Matsuzawa (eds), *The Mind of Chimpanzees.* Chicago and London: University of Chicago Press, pp. 116–25.

_____ and T. Matsuzawa. 2001. 'Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Cote d'Ivoire, West Africa', *Folia Primatologica* 72: 57–68.

_____ and T. Matsuzawa. 2002. 'Ant Dipping among the Chimpanzees of Bossou, Guinea, and Comparisons with Other Sites', *American Journal of Primatology* 58: 133–48.

_____ and T. Matsuzawa. 2004. 'Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa', *International Journal of Primatology* 25: 551–81.

_____ and C.T. Snowdon. 2008. 'Socially Biased Learning in the Acquisition of a Complex Foraging Task in Juvenile Cottontop Tamarins (*Saguinus oedipus*)', *Animal Behavaviour* 75: 267–77.

_____.C.T. Snowdon and T. Matsuzawa. 2009. 'Social Influences on Ant-dipping Acquisition in the Wild Chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa', *Animal Cognition* 12: S37–S48.

Ingold, T. 2001. 'The Use and Abuse of Ethnography', *Behavioral and Brain Science* 24: 337.

Inoue-Nakamura, N. and T. Matsuzawa. 1997. 'Development of Stone Tool Use by Wild Chimpanzees (*Pan troglodytes*)', *Journal of Comparative Psychology* 111: 159–73.

Jaeggi, A.V., L.P. Dunkel, M.A. van Noordwijk, S.A. Wich, A.A.L. Sura and C.P. van Schaik. 2010. 'Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture, *American Journal of Primatology* 72: 62–71.

_____.L. Dunkel and C.P. van Schaik. 2007. 'The Role of Social Learning in the Acquisition of Foraging Skills in Wild Bornean Orang-utans (*Pongo pygmaeus*)', *American Journal of Physical Anthropology* Suppl. 44: 135.

Kant, I. 1786. 'Mutmasslicher Anfang der Menschengeschichte', *Berlinische Monatschrift* 176: 1–27.

Kawamura, S. 1959. 'The Process of Sub-cultural Propagation among Japanese Macaques, *Primates* 2: 43–60.

Kendal, R.L. 2008. 'Animal "Culture Wars"', *The Psychologist* 21: 312–15.

Koops, K., W.C. McGrew and T. Matsuzawa. 2008. *Nut-cracking and the Chimpanzees of the Nimba Mountains, Guinea, West Africa: An Experimental Approach to the Study of Ape Technology*, International Primatological Society. Edinburgh: Primate Eye-PSGB, Abst #395.

Kroeber, A.L. 1928. 'Sub-human Culture Beginnings', *Quaterly Review of Biology* 3: 325–42.

_____ and C. Kluckhohn. 1952. 'Culture: A Critical Review of Concepts and Definitions', *Papers of the Peabody Museum of American Archaeology and Ethnology* 47: 1–223.

Kummer, H. 1971. *Primate Societies: Group Techniques of Ecological Adaptation.* Chicago: Aldine.

Laland, K.N. and W. Hoppitt. 2003. 'Do Animals have Culture?', *Evolutionary Anthropology* 12: 150–59.

_____ and V.M. Janik. 2006. 'The Animal Cultures Debate', *Trends In Ecology and Evolution* 21: 542–47.

_____ and J.R. Kendal. 2003. 'What the Models say about Animal Social Learning', in D.M. Fragaszy and S. Perry (eds), *The Biology of Traditions: Models and Evidence*. Cambridge: Cambridge University Press, pp. 33–55.

Leca, J.B., N. Gunst and M.A. Huffman. 2007. 'Japanese Macaque Cultures: Inter- and Intra-troop Behavioural Variability of Stone Handling Patterns across 10 Troops', *Behaviour* 144: 251–81.

Lind, J. and P. Lindenfors. 2010. 'The Number of Cultural Traits Is Correlated with Female Group Size but Not with Male Group Size in Chimpanzee Communities', *PLoS One* 5: e9241.

Lonsdorf, E.V. 2006. 'What is the Role of Mothers in the Acquisition of Termite-fishing Behaviors in Wild Chimpanzees (*Pan troglodytes schweinfurthii*)?', *Animal Cognition* 9(1): 36–46.

_____ and K.E. Bonnie. 2010. 'Opportunities and Constraints when Studying Social Learning: Developmental Approaches and Social Factors'. *Learning and Behavior* 38(3): 195–205.

Lycett, S.J. 2010. 'The Importance of History in Definitions of Culture: Implications from Phylogenetic Approaches to the Study of Social Learning in Chimpanzees', *Learning and Behavior* 38(3): 252–64.

_____.2011. '"Most Beautiful and Most Wonderful": Those Endless Stone Tool Forms', *Journal of Evolutionary Psychology* 9(2): 143–71.

_____.M. Collard and W.C. McGrew. 2007. 'Phylogenetic Analyses of Behavior Support Existence of Culture among Wild Chimpanzees', *Proceedings of the National Academy of Sciences of the United States of America* 104(45): 17588–92.

_____.M. Collard and W.C. McGrew. 2010. 'Are Behavioral Differences among Wild Chimpanzee Communities Genetic or Cultural? An Assessment Using Tool-use Data and Phylogenetic Methods', *American Journal of Physical Anthropology* 142(3): 461–67.

Mannu, M. and E.B. Ottoni. 2009. 'The Enhanced Tool-kit of Two Groups of Wild Bearded Capuchin Monkeys in the Caatinga: Tool Making, Associative Use and Secondary Tools', *American Journal of Primatology* 71(3): 242–51.

Matsuzawa, T. 1994. 'Field Experiments on Use of Stone Tools by Chimpanzees in the Wild', in R.W. Wrangham, W.C. McGrew, F.B.M. de Waal and P.G. Heltne (eds), *Chimpanzee Cultures*. Cambridge: Harvard University Press, pp. 351–70.

_____.D. Biro, T. Humle, N. Inoue-Nakamura, R. Tonooka, G. Yamakoshi and T. Matsuzawa. 2001. 'Emergence of Culture in Wild Chimpanzees: Education by Master-apprenticeship', in T. Matsuzawa (ed.), *Primate Origins of Human Cognition and Behavior.* Tokyo: Springer-Verlag, pp. 557–74.

_____.T. Humle and Y. Sugiyama (eds). 2011. *The Chimpanzees of Bossou and Nimba*. Tokyo: Springer-Verlag.

_____ and W.C. McGrew. 2008. 'Kinji Imanishi and 60 years of Japanese Primatology', *Current Biology* 18(14): R587–R591.

McGrew, W.C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution.* Cambridge: Cambridge University Press.

_____ 2003. 'Ten Dispatches from the Chimpanzee Culture Wars', in F.B.M. de Waal and P.L. Tyack (eds), *Animal Social Complexity Intelligence, Culture and Individualized Societies*. Cambridge: Havard University Press, pp. 419–39.

_____.R.M. Ham, L.J.T. White, C.E.G. Tutin and M. Fernandez. 1997. 'Why Don't Chimpanzees in Gabon Crack Nuts? *International Journal of Primatology* 18: 353–74.

_____ and C.E.G. Tutin. 1978. 'Evidence for a Social Custom in Wild Chimpanzees?', *Man* 13(2): 234–51.

Mercader, J., H. Barton, J. Gillespie, J. Harris, S. Kuhn, R. Tyler and C. Boesch. 2007. '4,300-year-old Chimpanzee Sites and the Origins of Percussive Stone Technology', *Proceedings of the National Academy of Sciences of the United States of America* 104(9): 3043–48.

_____.M. Panger and C. Boesch. 2002. 'Excavation of a Chimpanzee Stone Tool Site in the African Rainforest', *Science* 296: 1452–55.

Mobius, Y., C. Boesch, K. Koops, T. Matsuzawa and T. Humle. 2008. 'Cultural Differences in Army Ant Predation by West African Chimpanzees? A Comparative Study of Microecological Variables', *Animal Behaviour* 76: 37–45.

Nakamura M. and S. Uehara. 2004. 'Proximate Factors of Two Types of Grooming-hand-clasp in Mahale Chimpanzees: Implication for Chimpanzee Social Custom', *Current Anthropology* 45(1):108–14.

Ottoni, E.B. and P. Izar. 2008. 'Capuchin Monkey Tool Use: Overview and Implications', *Evolutionary Anthropology* 17(4): 171–78.

Panger, M.A., S. Perry, L. Rose, J. Gros-Louis, E. Vogel, K.C. Mackinnon and M. Baker. 2002. Cross-site Differences in Foraging Behavior of White-faced Capuchins (*Cebus capucinus*), *American Journal of Physical Anthropology* 119(1): 52–66.

Perry, S. 2009. 'Conformism in the Food Processing Techniques of White-faced Capuchin Monkeys (*Cebus capucinus*)', *Animal Cognition* 12(5): 705–16.

_____.M. Baker, L. Fedigan, J. Gros-Louis, K. Jack, K.C. MacKinnon, J.H. Manson, M. Panger, K. Pyle and L. Rose. 2003. 'Social Conventions in Wild White-faced Capuchin Monkeys – Evidence for Traditions in a Neotropical Primate', *Current Anthropology* 44(2): 241–68.

Sanz, C.M. and D.B. Morgan. 2007. 'Chimpanzee Tool Technology in the Goualougo Triangle, Republic of Congo', *Journal of Human Evolution* 52(4): 420–33.

_____ and D.B. Morgan. 2009. 'Flexible and Persistent Tool-using Strategies in Honey-gathering by Wild Chimpanzees', *International Journal of Primatology* 30(3): 411–27.

_____ C. Schoning and D.B. Morgan. 2010. 'Chimpanzees Prey on Army Ants with Specialized Tool Set', *American Journal of Primatology* 72(1): 17–24.

Schaik, C.P. van, M. Ancrenaz, G. Borgen, B. Galdikas, C.D. Knott, I. Singleton, A. Suzuki, S.S. Utami and M. Merrill. 2003a. 'Orangutan Cultures and the Evolution of Material Culture', *Science* 299(5603): 102–5.

_____ E.A. Fox, and L.T. Fechtman. 2003b. 'Individual Variation in the Rate of Use of Tree-hole Tools among Wild Orangutans: ImSchoning, C., T. Humle, Y. Mobius and W.C. McGrew. 2008. 'The Nature of Culture: Technological Variation in Chimpanzee Predation on Army Ants Revisited', *Journal of Human Evolution* 55(1): 48–59.

Sousa, C., D. Biro and T. Matsuzawa. 2009. 'Leaf-tool Use for Drinking Water by Wild Chimpanzees (*Pan troglodytes*): Acquisition Patterns and Handedness', *Animal Cognition* 12: S115–S125.

Tomasello, M. 1999. *The Cultural Origins of Human Cognition.* Cambridge, MA: Harvard University Press.

Tonooka, R. 2001. 'Leaf-folding Behavior for Drinking Water by Wild Chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea', *Animal Cognition* 4: 325–34.

Tyler, E.B. 1871. *Primitive Culture.* London: Murray.

Visalberghi, E., D. Fragaszy, E. Ottoni, P. Izar, M.G. de Oliveira and F.R.D. Andrade. 2007. 'Characteristics of Hammer Stones and Anvils Used by Wild Bearded Capuchin Monkeys (*Cebus libidinosus*) to Crack Open Palm Nuts, *American Journal of Physical Anthropology* 132(3): 426–44.

Voelkl, B and L. Huber. 2000. 'True Imitation in Marmosets', *Animal Behaviour* 60: 195–202.

Waal, F.B.M. de. 1999. 'Cultural Primatology Comes of Age', *Nature* 399: 635–36.

Watson, C.F.I. and C.A. Caldwell. 2009. 'Understanding Behavioral Traditions in Primates: Are Current Experimental Approaches too Focused on Food?', *International Journal of Primatology* 30(1): 143–67.

Whiten, A., J. Goodall, W.C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C.E. Tutin, R.W. Wrangham and C. Boesch. 1999. 'Cultures in Chimpanzees', *Nature* 399(6737): 682–85.

_____.J. Goodall, W.C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C.E. Tutin, R.W. Wrangham and C. Boesch. 2001. 'Charting Cultural Variation in Chimpanzees', *Behaviour* 138: 1481–516.

_____.V. Horner, C.A. Litchfield and S. Marshall-Pescini. 2004. 'How do Apes Ape?', *Learning Behavaviour* 32(1): 36–52.

Wich, S.A., S.S. Utami Atmoko, T. Mitra Setia and C.P. van Schaik (eds). 2009. *Orangutans: Geographic Variation in Behavioral Ecology and Conservation.* Oxford: Oxford University Press.

Wrangham, R.W., F.B.M. de Waal and W.C. McGrew. 1994. 'The Challenge of Behavioral Diversity', in R.W. Wrangham, W.C. McGrew, F.B.M. de Waal, P.G. Heltne and L.A. Marquardt (eds), *Chimpanzee Cultures.* Cambridge: Harvard University Press, pp. 1–18.

Yamakoshi, G. and Y. Sugiyama. 1995. 'Pestle-pounding Behavior of Wild Chimpanzees at Bossou, Guinea: A Newly Observed Tool-using Behavior', *Primates* 36(4): 489–500.